TEMPORAL AND SPATIAL DISTRIBUTION OF THE RARE, MYRMECOPHAGOUS ILLIDGE'S ANT-BLUE BUTTERFLY, *ACRODIPSAS ILLIDGEI* (LYCAENIDAE)

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ABSTRACT. A survey of 591 branch sections containing arboreal ant colonies on 197 trees was undertaken over four consecutive seasons for the presence of immature *Acrodipsas illidgei* (Waterhouse and Lyell) in and adjacent to mangroves at Mary River Heads, Queensland, Australia. *A. illidgei* was found in 1.7% of ant colony sections sampled (i.e., 10 colony sections on five *Avicennia marina* (Forssk.) trees). Despite the small number of immatures discovered, *A. illidgei* showed a strong tendency to occur in specific ant colonies over time. The host ant, *Crematogaster* sp. (*laeviceps* group F. Smith) (Formicidae: Myrmicinae), was common and widespread within the survey area. The mean seasonal level of adult ant activity outside the nest positively correlated to mean seasonal ant brood levels within nests but were significantly linked only in spring and autumn. New information supports the hypothesis that ant colony odour selection by ovipositing female *A. illidgei* is the prime influence on this butterfly's localized distribution.

Additional key words: localized distribution, conservation, mangrove, *Crematogaster*, Australia.

The genus *Acrodipsas* Sands (Lycaenidae: Theclinae) is unique to Australia and contains eight described and at least one undescribed species (Sands et al. 1997, Sands, pers. comm.). All *Acrodipsas* species are known or suspected to have larvae that feed on ants (Sands 1979, Common & Waterhouse 1981). *Acrodipsas illidgei* (Waterhouse & Lyell) has an obligate, myrmecophagous relationship with the arboreal ant, *Crematogaster* sp. (*laeviceps* group F. Smith) (Formicidae: Myrmicinae), in or adjacent to mangrove habitats (Smales & Ledward 1942, Samson 1987, Beale & Zalucki 1995).

Ant-attended lycaenids such as *Acrodipsas* species in Australia (Common & Waterhouse 1981) and *Maculinea* species in Europe (Thomas et al. 1989, Thomas & Wardlaw 1990) often occur naturally at low abundance (Pierce et al. 1987, see also review in Walter & Zalucki 1998) in small, semi-isolated demes (Pierce 1984). Curiously, *A. illidgei* does not appear to have specific requirements restricting it to its known habitat, though it depends directly on the presence of its host ant species, which may be found in greatest abundance in and around mangrove environments. Although distribution is not restricted by plant species associations (immatures have been found in ant colonies on grey mangrove, *Avicennia marina* (Forssk.) Vierh. (Avicenniaceae) in mangroves, and on swamp oak, *Allocasuarina glauca* (Sieger ex Sprengal) (Casuarinacae), and *Eucalyptus* sp. (Myrtaceae) adjacent to mangroves) and its host ant is widespread and abundant, its low relative abundance seems to be maintained primarily by regular bouts of host ant aggression and the carrying capacity of colonies (Beale & Zalucki 1995).

Except for host ant induced mortality, the larval and pupal stages occupy an 'enemy-free' space (see Lawton 1978, Atsatt 1981a) once neonates are carried back to the nest. Unlike some myrmecophagous lycaenids such as *Liphyra brassolis major* Rothchild (Dodd 1902), and myrmecophilous species (Malicky 1970), larvae of *A. illidgei* have an epidermis containing numerous glands (Samson 1989, see also review by Fiedler et al. 1996), which is easily pierced by its small, aggressive host species. According to Malicky (1970), a thick cuticle of the larval integument is a typical lycaenid adaptation against ant mandible damage, yet even mature *A. illidgei* larvae apparently lack this defence against an ant species with which it shares a highly specific relationship. The nature of this ant/butterfly relationship raises the question: are immature *A. illidgei* completely reliant upon chemical mimicry for survival, and if so, are females selecting local 'home' ant colonies because of 'host conditioning' or 'adult emergence experience' (Hopkins 1917, see review by Mackenzie 1992)?

The purpose of this study is to determine the distribution of *A. illidgei* host ant colonies over time and assess whether *A. illidgei* is host ant colony specific. The relevance of the findings to the conservation status of *A. illidgei* is discussed.

STUDY SITES AND METHODS

Sections of *Crematogaster* sp. (*laeviceps* group) colonies in branches (one branch/tree sampled) of grey mangrove, *A. marina*, and non-mangrove species were sampled at the site of a recently discovered population of *A. illidgei* (Manskie & Manskie 1989), Mary River Heads (25°38'S, 152°38'E) in south-east Queensland, over a 10 month period beginning in August 1994 (see Figs. 1, 2). Field trips were made to Mary River Heads on 19–20 September 1994 (winter), 16–19 November 1994 (spring), 21–23 February 1995 (summer), and 15–19 May 1995 (autumn). The first survey included tagging, mapping and data collection from 183 *A. marina* and 14 landward *A. glauca* and *Eucalyptus* species. Sampling was carried out in four sectors, two on the eastern side and two on the western side of the River Heads peninsula (Fig. 2).

A subset of trees were selectively sampled in a haphazard manner for chambered branches of a minimum thickness (≥10 mm) containing a section of *Crematogaster* ant nest to maximize chances of encountering *A. illidgei*. Previous studies (Beale & Zalucki 1995) indicated that branches below a minimum thickness were unlikely to possess chambers suitable for *Crematogaster* ants and therefore even less likely to contain *A. illidgei*. Most *A. marina* trees were located on or just inside the seaward edge beyond large stands of red mangrove, *Rhizophora stylosa* Griff., and yellow mangrove, *Ceriops* sp. (both Rhizophoraceae), and
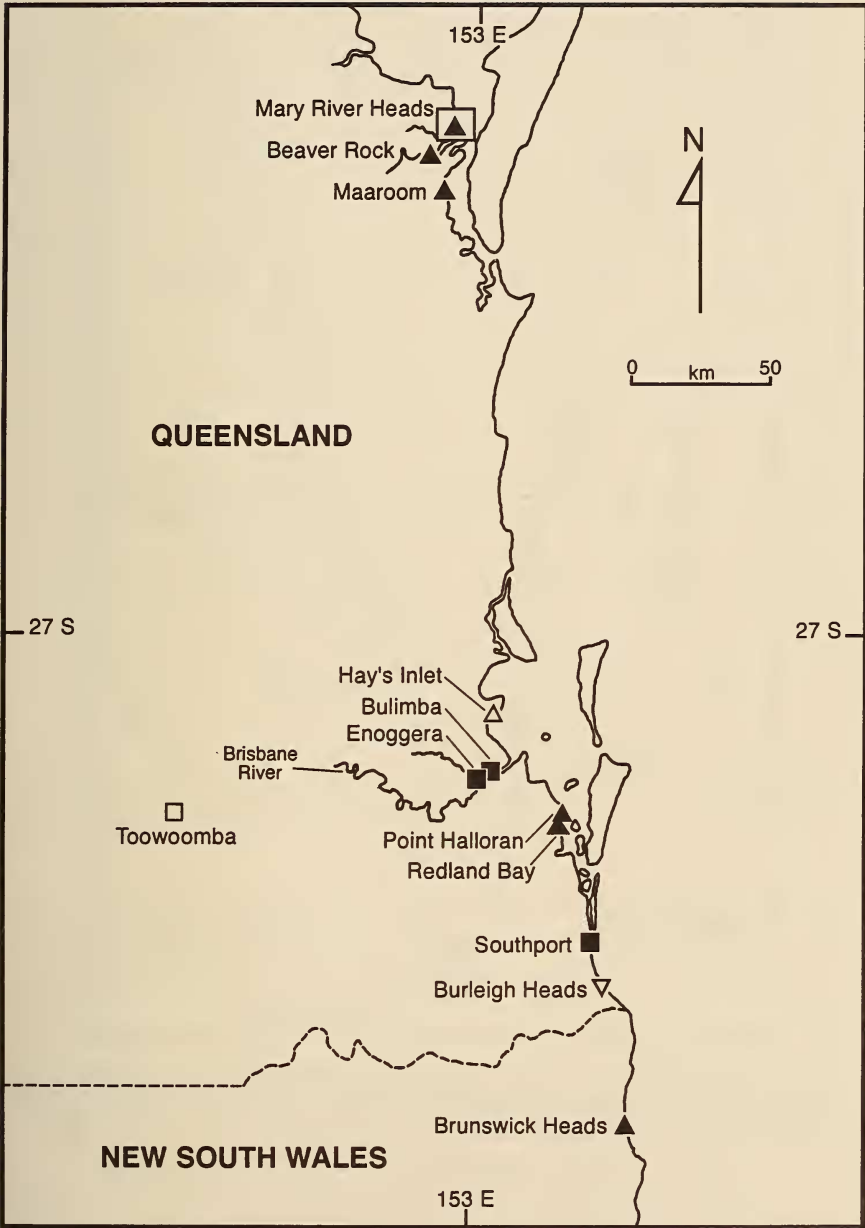
Fig. 1. Status of historical populations of *Acrodipsas illidgei*: filled upward triangle = recorded since 1985, habitat largely intact; open upward triangle = recorded before 1985, habitat largely intact; open square = requires confirmation; filled squared = population almost certainly extinct; open downward triangle = status unclear, threatened or extinct. Boxed area at Mary River Heads is location of study area in Fig. 2.
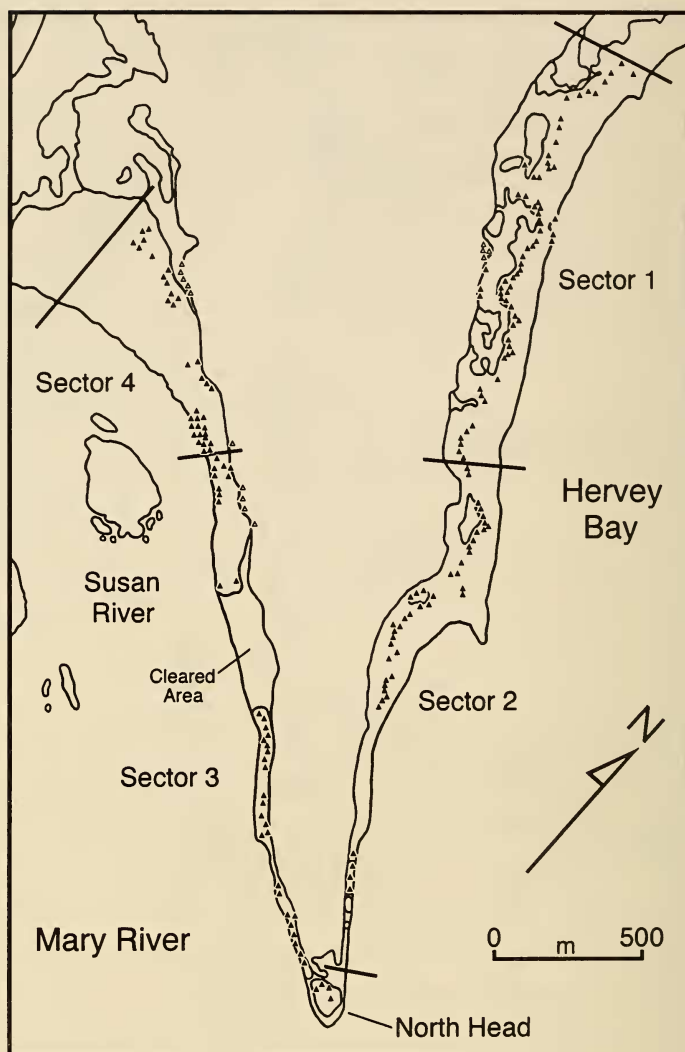
FIG. 2.   Map of Mary River Heads field site showing distribution of sampled *Avicennia marina* trees (filled triangles) and non-mangrove tree species including *Allocasuarina* sp. and *Eucalyptus* sp. (open triangles).

river mangrove, *Aegiceras corniculatum* (L.) Blanco (Myrsinaceae). Sampled trees were mapped onto enlarged aerial photographs.

   Data collected from each tree included tree height, number of chambered branches/tree, position of tree (edge/non-edge, where edge = at least one side of a tree is facing a clearing, landward or seaward edge),
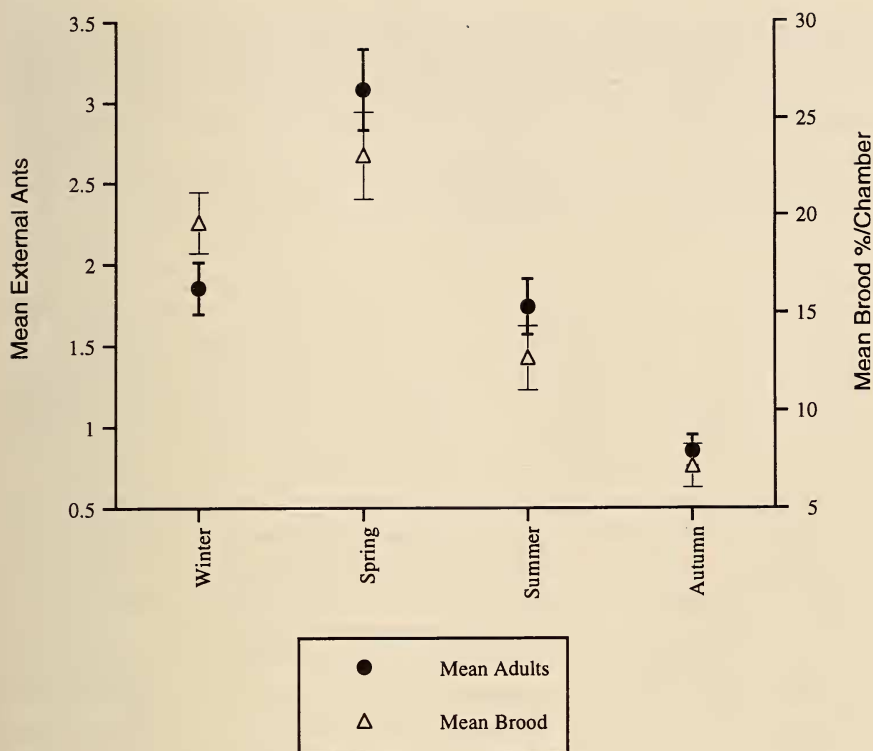
FIG. 3.   Graphs showing mean number of external ants and mean ant brood percent per brood chamber in each season at Mary River Heads.

the height of the sampled chambered branch, and the external ant activity adjacent to sampled chambered branch (ants/10 cm of ant trail) (Fig. 3). Chambered branches were split and examined *in situ* for about 5 to 10 minutes each. Chambered branch measurements included length and diameter; the presence or absence of *A. illidgei* immatures and stage present; the presence of other lycaenid butterfly immatures; and amount of ant brood as a volume/chambers in chambered branches as a percentage. Ant specimens were identified and compared by S. O. Shattuck (Australian National Insect Collection, CSIRO, Canberra). Many sampled branches (n = 153) were repaired up to three times each with wire and re-attached to the tree close to where they had been removed. Fourteen landward trees (13 *Allocasuarina glauca*, 1 *Eucalyptus* sp.) were sampled and mapped in the same manner as mangrove trees although their position (i.e., edge/non-edge) was not recorded. The probability of host trees possessing *A. illidgei* immatures in recorded se-

quences was calculated. Summary statistics of the complete dataset for adult ant activity and percentage ant brood per chamber are presented as means ± standard errors with analysis of data using ANOVA and graphed. Data from trees which were sampled in every season was categorized and tested for independence using chi-square (i.e., categories of adult ants: 0, 1, 2, ≥ 3/10 cm; categories for percentage ant brood/ sampled chambers: low < 10%, medium = 10–40%; high > 40%).

RESULTS

The total number of samples taken from the 183 *A. marina* trees over each season was 554 (many repaired branches resampled up to three times) while 14 non-mangrove species were sampled a total of 37 times. Trees sampled in all four seasons totalled 87. Immature stages of *A. illidgei* occurred in only 10 ant colony sections on five *A. marina* trees among 197 trees sampled (1.7%, Table 1). Four ant colony sections containing immatures were found in both winter and spring, while one was discovered in summer and again in autumn. Sector 1 had immatures in a single landward edge tree in every season, and this same colony possessed two larvae in 1992 (Beale & Zalucki 1995). One tree in Sector 3 possessed immatures in winter and spring only. A single tree in Sector 3 possessed an empty pupal case in winter and a fifth instar larva in spring. Another tree in Sector 4 contained one third instar larva in both winter and spring. No *A. illidgei* immatures were discovered in Sector 2 (Fig. 2). The particular immature stages or instars present in subsequent samples on the same trees indicated that they represented separate generations. There was a tendency for immatures to occur in the same ant colonies over time (Table 1). Cumulative sampling impact meant that only one in five branch sections could be expected to contain ants after four (i.e., three repairs) consecutive samples (Beale & Seeman, unpubl. data).

Although only five trees contained *A. illidgei*, they displayed variation of attribute measurements consistent within the overall sample. For example, host trees in Sectors 3 (host tree heights = 390 cm, 410 cm, 560 cm) and Sector 4 (650 cm) (Fig. 2) were of taller and denser habit than the host tree found in Sector 1 (250 cm). The mean and range of host tree attributes included; a height of 452 cm (250–650 cm); sampled branch height of 164 cm (120–220 cm); sampled branch length of 52 cm (27–120 cm); sampled branch diameter of 22 mm (15–28 mm); and four (1–7) chambered branches per tree. Sixty percent (i.e., three out of five) of host trees were situated on the edge of mangrove vegetation.

Ant specimens from Mary River Heads and Redland Bay proved to be morphologically indistinguishable (S. O. Shattuck, pers. comm.). External ant activity on tree trunks adjacent to sampled colonies varied significantly between all seasons (summer and autumn, p = 0.0016; winter

TABLE 1.   Persistence of immature stages of *Acrodipsas illidgei* in sampled sections of *Crematogaster* sp. (*laeviceps* group) colonies in *Avicennia marina*. Dashes in table indicate no ant colony section accessible and therefore no sample able to be taken from tree at this time. p refers to probability of host tree being positive for *A. illidgei* in the listed sequence over all seasons (except where not sampled) assuming that each sample is independent.

| Host tree # | Season | | | | p |
	Winter	Spring	Summer	Autumn	
1	1	1	1	1	<0.0001
2	1	—	—	—	0.0219
3	1	1	0	—	0.0007
4	1	1	0	0	0.0007
5	0	1	0	0	0.0320
Total host trees	4	4	1	1	0.0553
Total trees sampled	183	120	112	129	—

and spring, spring and summer, p < 0.0001) except summer and winter (p = 0.58). A prominent peak in external ant activity on trees was noticed during the spring (mean = 3.1, SE = 0.26, n = 120) as compared to winter (mean = 1.9, SE = 0.16, n = 183), summer (mean = 1.7, SE = 0.171, n = 112) and autumn (mean = 0.9, SE = 0.1, n = 106). Similarly, percentage ant brood/chamber occupied varied seasonally (p < 0.03) except between winter and spring (p = 0.108) (Fig. 3). The spring peak (χ^2 = 14.02, df = 6, p < 0.03) and autumn level (χ^2 = 17.236, df = 6, p < 0.01) in external ant numbers corresponded to percentage ant brood in chambered branches during the same seasons but this was not the case in winter (χ^2 = 2.965, df = 6, p > 0.8) and summer (χ^2 = 6.246, df = 6, p = 0.39).

DISCUSSION

Localized distributions are common among myrmecophilous lycaenids but these are thought to be largely dependent on the overlapping distributions of the attending ant and host plant species (e.g., Smiley et al. 1988, Seufert & Fiedler 1996), the presence of conspecifics or other species (e.g., Webster & Nielsen 1984) or a combination of factors including plant quality (i.e., nitrogen content) (e.g., Pierce 1984, Thomas 1985, Baylis & Pierce 1991). Superficially, the life history of *A. illidgei* seems uncomplicated, with its larvae predominantly feeding upon the immature stages of a common mangrove ant. However, individuals are extremely difficult to locate during any part of their life cycle, are found in extremely low densities during all stages of their development, and seem to be almost certainly restricted to specific host ant colonies. The distribution of ant colonies harbouring *A. illidgei* could be the result of a specific colony recognition by ovipositing females or reflect a high mortality rate in most potential colonies.

Sampling effects were minimized as much as possible during this study but reduced the chances of encountering immature stages in the same ant colony sections during follow up re-samples. The impact of sampling for *A. illidgei* immatures made whole ant colony investigations not only impractical, but undesirable. Cumulative damage to ant colony sections in winter and spring may account for three positive colony sections (i.e., host trees) subsequently becoming negative in the summer sample (Table 1). Despite this impact, consecutive positive samples (up to four after a positive sample two years earlier) indicate a strong persistence of *A. illidgei* in particular host colonies.

Data obtained from host colony sections and trees displayed variation consistent with that found in the overall sample and suggests that despite most trees appearing to be potential hosts for *A. illidgei*, this is rarely the case. A comparison of the two most 'successful' host ant colonies shows that one tree (in Sector 1) occurred in a less densely vegetated area and possessed a smaller, more spindly growth habit (i.e., more branches of smaller dimensions) when compared to the other (Sector 4) in an *A. marina* dominated zone. Similarly, the few positive samples suggest that host colonies are not necessarily confined to trees on the edge of the mangrove forest (where mean ant colony brood volume was significantly higher at Redland Bay) as previously supposed (Beale & Zalucki 1995, see also descriptions of 'edge effects' in Courtney & Courtney 1982).

The only obvious habitat requirement restricting *A. illidgei* appears to be the host ant, *Crematogaster* sp. (*laeviceps* group), a common and dominant taxonomic (i.e., morphological) species at least in surveyed mangrove forests. At Redland Bay, for example, 85% (n = 93) of grey mangrove harboured *Crematogaster* sp. (*laeviceps* group) ants (Beale, unpubl. data). The presence of cryptic (refer to Paterson 1991) *Crematogaster* species has not been ruled out but it seems unlikely that the presence of such a cryptic species could explain the butterfly's persistence in a handful of colonies, unless of course the ant species was similarly rare and localized.

Females of *A. illidgei* may require highly specific (i.e., chemical) oviposition cues or alternatively have a tendency not to be 'choosey' when selecting ant inhabited oviposition sites, resulting in a small proportion of individuals surviving in specific, accommodating ant colonies. The presence of a highly specific oviposition system seems most likely. Other (phytophagous) myrmecophilous species are known to select oviposition sites by using the correct ant species as a cue (Atsatt 1981b, Pierce & Elgar 1985, Fiedler & Maschwitz 1989). A highly specific and obligatory relationship with an ant species is typically associated with a highly specialized larval communication system (Fiedler et al. 1996) and this

would be expected to be most pronounced in a species like *A. illidgei*. It is reasonable to suggest that a highly specific larval/ant communication system would be initiated by a comparative level of chemical identification during oviposition, because when a 'good' choice is made, the host colony then becomes more of an enemy-free space (see below). This is not unlike conspecific *Crematogaster* sp. (*laeviceps* group) ants readily differentiating members of the same and different colonies, and behaving accordingly (Beale & Zalucki 1995). Although not direct evidence for specific colony selection behaviour, Samson (1989) observed that most trees harbouring the host ant did not possess eggs of *A. illidgei*, but aggregations of eggs (up to 25 eggs) were present on a few. Oviposition behaviour may be influenced by larval experience and conditioning (e.g., Schweissing & Wilde 1979) or 'adult emergence experience' or initial adult experience (Jaenike 1983, Papaj 1986, Prokopy & Fletcher 1987, Firempong & Zalucki 1991, Cunningham et al. 1998) because adults emerge from within the colony.

The nature of Illidge's ant-blue's/ant relationship is relevant to its overall mortality and therefore colony selection, because it requires either the chemical assimilation of larvae and/or the provision of much sought after bribes for ants, since parasitic larvae possess little physical defence against attack from a typically aggressive ant species. Furthermore, the loss of ant brood is unlikely to be offset by the potential for non-essential chemical benefits provided by *A. illidgei* larvae, if larvae are primarily myrmecophagous as they appear to be. Crypsis can be ruled out since the host ants actively carry neonates back to the colony where they are placed in among the ant's brood (Samson 1989); a very different behaviour to that exhibited towards the phytophagous lycaenid, *Ogyris amaryllis*, which provides the same ants with sugar secretions away from the nest. Colony carrying capacity (i.e., brood volume), although seemingly of great importance to butterfly survival, may not be relevant to colony selection because it cannot be accurately determined from outside the nest, although seasonally (i.e., in spring and autumn) external adult ant activity does appear to be linked to ant brood volume.

CONSERVATION OF *ACRODIPSAS ILLIDGEI*

Illidge's ant-blue provides an example of the dilemma facing researchers studying hard-to-find and potentially threatened insect species. Because only a few specimens at most are likely to be discovered during even a large study, it is difficult to justify the expenditure of resources for further research, relegating unusual species like *A. illidgei* to relative scientific obscurity. Transect counts for *A. illidgei* are likely to record many zeros and only occasional suspected sightings, and would be difficult to implement due to the inaccessibility of much of the dense,

mangrove vegetation. Furthermore, overestimates of distribution and density may occur if the status of A. *illidgei* is based principally upon a census of apparently abundant habitat resources. Hence, it is impractical to accurately monitor A. *illidgei* for anything other than its presence and even then, it can be easily overlooked.

Butterfly monitoring schemes in the United Kingdom have revealed that it is usually the localized species that experience the most severe declines over time (Pollard & Eversham 1995). Even minor damage to Illidge's ant-blue's habitat may in fact seriously threaten a localized population when their host colony specificity is taken into account (and this is even more pronounced in small remnant populations). It is likely that A. *illidgei*, with its relatively weak flight, its tendencies to remain settled for long periods punctuated by short flights, and for the female to emerge with a fully developed egg load (Sands 1979), would have difficulty in colonizing other habitat patches.

Recent efforts to preserve habitat of the Eltham copper, *Paralucia pyrodiscus lucida* Crosby, at Eltham in Victoria (Braby 1987) and A. *illidgei* at Redland Bay and Mary River Heads (Fig. 1) have indicated that public interest in conservation of invertebrates has not necessarily relied upon the economic (e.g., tourism, trading) or aesthetic value of a given species. Exceptions to this include *Ornithoptera* from New Guinea, but even then, commercial value has been used as a means to a conservation end (Cherfas 1979, Pyle et al. 1981). Once the public at Redland Bay and Maryborough and Hervey Bay (both near Mary River Heads) had been made aware of the fascinating biology of the drab, rarely seen *Acrodipsas illidgei*, it then became the driving force behind the species' prominence and habitat preservation efforts. Consequently, an important initial step in insect and habitat conservation should be the elucidation of the biology of rare and threatened species, with the subsequent dissemination of such information in a digestible form to the community at large. This is especially relevant if government insect preservation policy, in effect, relies heavily upon the prohibition of collecting (see e.g., Beale 1998).

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